

Distribution and Fine Structure of Antennal Sensilla in Emerald Ash Borer (Coleoptera: Buprestidae)

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ABSTRACT The antennal sensilla of the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), were examined using scanning and transmission electron microscopy. Male and female antennae have a scape, pedicel, and nine flagellomeres. Both male and female antennae share five sensillum types: sensilla chaetica (mechanoreceptors), three types of sensilla basiconica (olfactory), and uniporous gustatory/taste sensilla. Apical depressions containing large sensory fields of uniporous sensilla were seen on the eight most distal flagellomeres of both sexes. Counts of sensillum types showed that males possessed significantly more uniporous sensilla than females. We hypothesize that antennal contact is important for mate recognition by male *A. planipennis*. The distal apices of the eight outer flagellomeres were seen to have “tufts” composed of two types of sensilla basiconica. A third type of sensilla basiconica was observed within the perimeter of the uniporous sensory fields. The structure and putative function of each sensillum type are discussed.

KEY WORDS sensilla chaetica, sensilla basiconica, uniporous sensilla, sensory fields, electron microscopy

The emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is native to eastern Asia. It was found attacking ash (Oleaceae, *Fraxinus* spp.) in Detroit, MI, and Windsor, ON, Canada in 2002 (Haack et al. 2002). Since these initial detections, it has become a serious pest and has subsequently been found in Ohio and Maryland (2003), Indiana (2004), Illinois (2006), and Pennsylvania and West Virginia (2008; <http://www.emeraldashborer.info>). The life cycle of emerald ash borer within the United States seems to be similar to that described by Chinese scientists (Chinese Academy of Science, Institute of Zoology 1986, Yu 1992) and has been recently summarized by Poland and McCullough (2006a).

Being a relatively new invasive pest to North America and a minor pest within its native eastern Asia range (Yu 1992), there are few studies examining the chemical ecology of *A. planipennis*. Recent studies (Rodriguez-Saona et al. 2006; Crook et al. 2006, 2008) have begun to elucidate tree–insect interactions with respect to both leaf and bark volatiles. There is currently no evidence that *A. planipennis* has an attractive long-range sex pheromone (Otis et al. 2005). Recent behavioral studies have shown that *A. planipennis* males find potential mates using visual rather than long-range olfactory cues (Lelito et al. 2007). This is also true for other buprestid species that have been studied (Carlson and Knight 1969, Gwynne and Rentz 1983).

The purpose of this study was to describe the types and distribution of sensilla of *A. planipennis* as a basis for further studies on the chemical ecology of this important invasive pest species.

Materials and Methods

Insects. Ash bark containing *A. planipennis* prepupae was collected in July 2005 from a site in the Whitmore Lake area of Michigan, where infested wood (brought in from the surrounding area) was processed and disposed. The infested bark was then taken to the USDA laboratory in Brighton, MI, where it was stored in a refrigerator unit at 5°C to suspend beetle development until adults were required. Late-instar larvae and pupae were carefully extracted from the outer bark before being shipped to the USDA APHIS, PPQ, CPHST lab at Otis ANGB, MA. Pupae were kept in a dark container at room temperature until they emerged 3 to 4 wk later. Adults were then fed fresh evergreen ash (*Fraxinus uhdei*) foliage in plastic 480-ml. drink cups (Solo, Urbana, IL), with water in 30 ml plastic cups fitted with a wick. Insects were fed for ten days before they were frozen and prepared for examination.

Scanning Electron Microscope Preparation. Isolated heads were mounted on specimen stubs with silver adhesive and coated in a Tousimis Samsputter 2a (Tousimis Research, Rockville, MD) with gold/palladium three times for 1 min. Specimens were rotated between each run to distribute coating equally and reduce subsequent charging. Specimens were coated without using freeze drying or critical point drying

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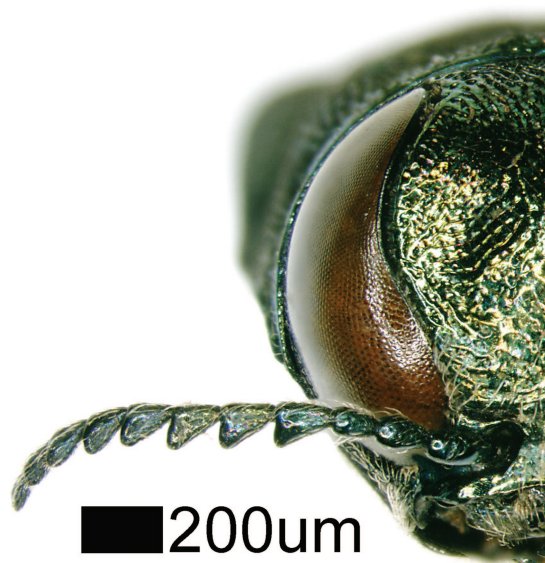


Fig. 1. Auto-montage (Syncroscopy) image of adult male *A. planipennis* showing typical alignment of antenna in relation to head.

techniques as these methods damage the antennal sensilla. Five beetles of each sex were examined with a JEOL JSM-840 scanning electron microscope (JEOL, Peabody, MA) at an accelerating voltage of 15 kV.

Transmission Electron Microscope (TEM) Preparation. Whole antennae were individually fixed for 1 h in 2.5% glutaraldehyde buffered in 0.13 M Millonig's phosphate buffer. The antennae were then washed in buffer, postfixed in aqueous 1% osmium tetroxide (OsO_4) for 2 h, dehydrated in a series of alcohols, and embedded in araldite epoxy resin for 24 h at 65°C. Silver sections were cut using a diamond knife (Diatome, EMS, Hatfield, PA), picked up on grids, stained with uranyl acetate and lead citrate, and examined on a 10CA TEM (Carl Zeiss Inc., Thornwood, NY). Micrographs were recorded with an AMT camera (Advanced Microscopy Techniques, Danvers, MA).

Results

Male and female antennae are almost identical in their size and structural configuration. Unless stated otherwise, the following description of the antennal morphology applies to both sexes. The antennae are situated between the compound eyes and curve down ventrally (Fig. 1). When stressed, the insect can rotate the antennae around its axis so that its curved shape lies dorsally flat over the back of the head. The curved antennae have 11 antennomeres. The first most proximal antennomere is the scape, which attaches the antenna to the head. This is followed by the pedicel and nine flagellomeres. These nine flagellomeres make up what is commonly referred to as the "antennal flagellum." Antennae look serrated due to the bilaterally flattened triangular shape of the most distal eight flagellomeres (Fig. 2). Total male length ($n = 3$)

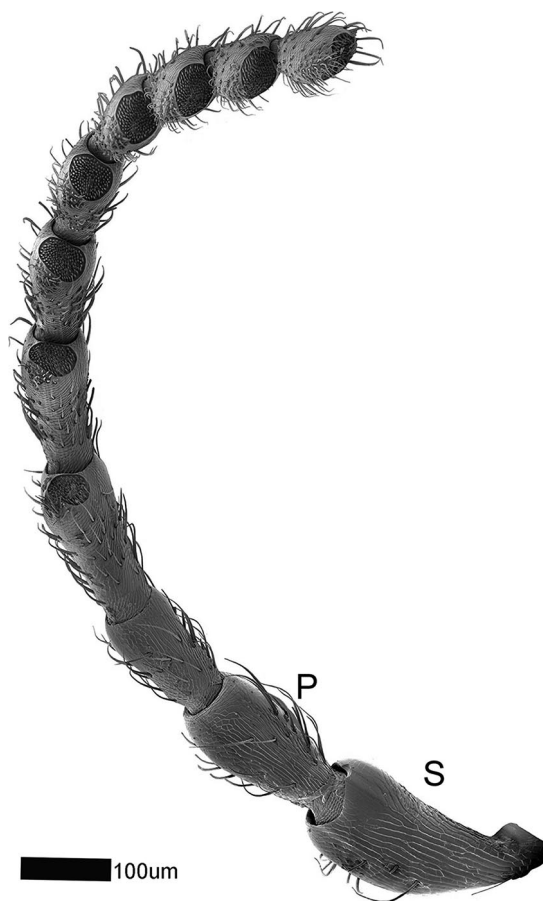


Fig. 2. Scanning electron micrograph of *A. planipennis* antenna (female). S, scape; P, pedicel.

was $2,320 \pm 25.16 \mu\text{m}$ compared with $2,381 \pm 64.62 \mu\text{m}$ for the female ($n = 5$). The scape is the longest part of the antenna, measuring 273 ± 12 and $332 \pm 8 \mu\text{m}$ for the male and female, respectively. The pedicel measures $220 \pm 0 \mu\text{m}$ for the male and $235 \pm 12.6 \mu\text{m}$ for the female. Flagellomeres are similar in shape, but the most distal eight, become progressively smaller toward the tip of the antenna (Fig. 2). The most proximal of these eight flagellomeres measures $243 \pm 6.6 \mu\text{m}$ for male and $263 \pm 11.13 \mu\text{m}$ for female antennae. The most proximal "tip" measures $170 \pm 0 \mu\text{m}$ on male and $165 \pm 11.8 \mu\text{m}$ on female antennae, respectively.

Types of Sensilla

Sensilla morphology is based upon common terminology used by Altner and Prillinger (1980) and Zacharuk (1980). Male and female antennae have five different types of sensilla; sensilla chaetica, sensilla basiconica (three types), and uniporous sensilla. Distributions and mean counts of all sensilla types on both male and female antennae are shown in Table 1.

Aporous Mechanoreceptor (Sensilla Chaetica). These sensilla are present along the entire length of the antennae of both male and female *A. planipennis*.

Table 1. Distribution and mean numbers (SD) of sensilla on the antennae of male *A. planipennis* ($n = 5$)

	Uniporous chemoreceptors		Sensilla basiconica type I		Sensilla basiconica type II		Sensilla basiconica type III		Sensilla chaetica	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
(Scape)	0	0	0	0	0	0	0	0	21 (6)	19 (1)
(Pedicel)	0	0	0	0	0	0	0	0	37 (9)	36 (5)
1	0	0	0	0	0	0	0	0	35 (7)	38 (4)
2	72 (14)	112 (15)**	2 (2)	1 (1)	7 (2)	8 (1)	10 (2)	10 (3)	48 (7)	42 (4)
3	98 (13)	137 (34)*	3 (3)	3 (1)	10 (2)	8 (2)	12 (2)	13 (2)	46 (6)	41 (4)
4	137 (16)	195 (18)*	6 (2)	5 (1)	10 (2)	9 (1)	10 (2)	13 (1)*	45 (6)	40 (4)
5	152 (21)	204 (30)*	7 (2)	4 (1)	10 (2)	8 (1)	11 (4)	14 (3)	43 (3)	43 (3)
6	151 (26)	186 (43)	9 (3)	7 (2)	10 (1)	10 (1)	10 (3)	13 (2)	41 (2)	37 (4)
7	178 (26)	231 (20)*	8 (2)*	5 (2)	10 (3)	12 (1)	14 (6)	17 (5)	42 (3)	38 (7)
8	157 (21)	199 (19)*	9 (4)	6 (1)	10 (1)	12 (2)	10 (3)	16 (2)*	40 (3)	35 (6)
9	136 (37)	119 (20)	9 (4)	6 (2)	11 (6)	18 (2)	22 (11)	21 (4)	41 (3)	38 (5)

* Asterisk (*) Indicates a significant difference in the number of sensilla between the sexes ($P < 0.05$; t -test).

They seem evenly distributed around the circumference of each flagellomere. These sensilla each have a membranous base and longitudinal ridges that run along their length to the tip (Figs. 3 and 4). These sensilla are usually $\approx 65 \mu\text{m}$ in length (ranging between 35 and $140 \mu\text{m}$) and are found in equal numbers ($P > 0.05$; t -test) on both male and female antennae (Table 1). The longer sensilla are located on the scape and may regulate movement/rotation of the entire antenna.

In section (Figs. 5 and 6) sensilla chaetica have a nonperforated wall and a single sensory neuron, the dendrite of which terminates in the form of a tubular body, at the side of the sensillum base. The tubular body (a mass of microtubules within an electron-dense material) represents the end of the sensory dendrite and interacts with the inner portion of the socket base.

Uniporous (Gustatory/Taste) Sensilla. These sensilla are short, smooth sided pegs $\approx 7\text{--}8 \mu\text{m}$ in length and $2 \mu\text{m}$ in diameter, with no distinct socket at their base. They are located within a crater like depression located on the distal surface of the outermost eight

flagellar subsegments (Fig. 7). Between 57 and 258 of these short structures are in each depression, giving these outer eight segments a “brush-like” appearance. These sensilla possess a single, oval-shaped pore at the distal tip (Fig. 8). A viscous exudate sometimes covers this external pore. Counts of these sensilla are lower on the two most proximal flagellar subsegments. Male antennae have significantly more of these sensilla when compared with females ($P < 0.05$; t -test) on every flagellomere except the tip (Table 1).

In section, these sensilla have a thick nonperforated wall ($0.5\text{--}1 \mu\text{m}$) and two non-branching sensory neurons, the dendrites of which extend up to the pore opening at the tip (Figs. 9 and 10). The lumen seems to be subdivided into two canals, each one being completely filled with a dendrite (Fig. 10).

Multiporous (Olfactory Chemoreceptor) Sensilla. For both sexes numbers of multiporous sensilla (per flagellomere) increased toward the distal tip of the antenna. There are three types of single-walled multiporous sensilla on the beetle antenna.

Sensilla Basiconica (Type I). These sensilla are the least abundant of all sensilla types seen on the antenna. These sensilla are smooth-sided pegs $\approx 12\text{--}16 \mu\text{m}$ in

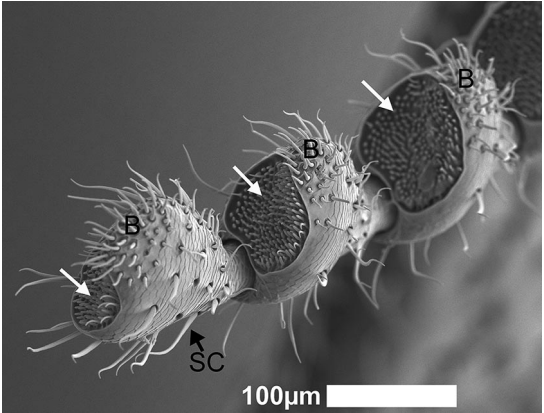


Fig. 3. Scanning electron micrograph of the three most distal antennal flagellomeres of a male *A. planipennis* antenna. White arrows indicate apical depressions or pits filled with numerous uniporous sensilla. Apical tufts of sensilla basiconica types II and III (B) sensilla chaetica (SC).

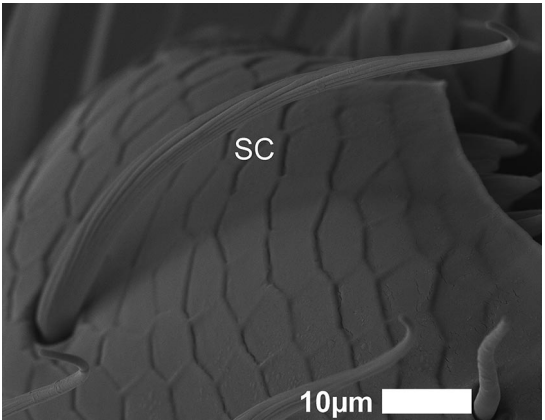


Fig. 4. Scanning electron micrograph of sensilla chaetica (SC) on the eighth flagellomere of a male *A. planipennis* antenna.

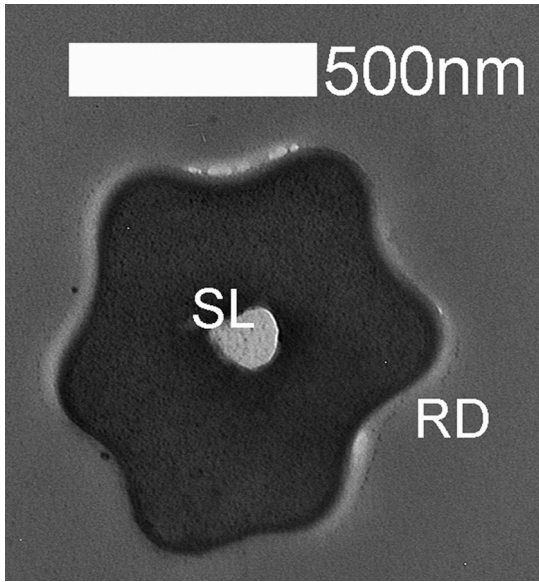


Fig. 5. Transmission electron micrograph of sensilla chaetica in *A. planipennis* male. Cross section cut $\approx 5\text{--}10\text{ }\mu\text{m}$ from the tip, shows ridged outer wall (RD) and a sensilla lumen (SL) free of dendritic material (magnification, $31,500\times$).

length and $1.5\text{--}2\text{ }\mu\text{m}$ in diameter, with no distinct socket at their base (Fig. 11). Between 1–15 of these sensilla are located within the distal “pit” of the outermost eight flagellomeres. They are situated along the edge of the numerous “fields” of uniporous sensilla (Fig. 7). Numbers per segment generally increase toward the distal tip of the antenna for both male and female *A. planipennis*, with numbers being similar for both sexes (Table 1).

In section, $\approx 1\text{--}2\text{ }\mu\text{m}$ beneath the hair shaft, there seem to be five sensory neurons encased in a dendritic sheath (Fig. 12). Up to 14 dendritic branches were observed in sections cut nearer the tip of a sensillum. Some

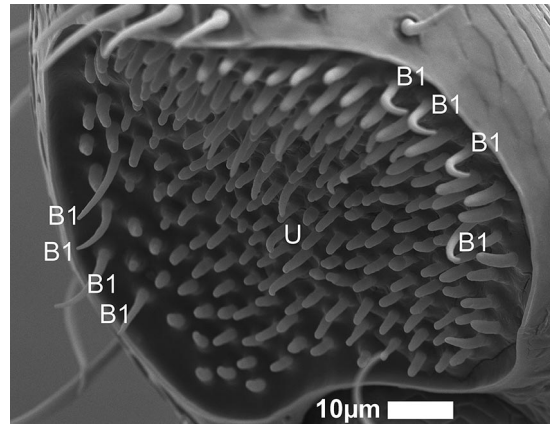


Fig. 7. Scanning electron micrograph showing the apical depression on the 10th flagellar segment of male *A. planipennis*. These apical depressions are located on the most distal eight flagellomeres. Each one contains a sensory field composed mainly of uniporous sensilla (U) with a few sensilla basiconica type I (B1) situated around the perimeter.

dendrites became swollen and seemed to fuse with each other, higher up toward the sensillum tip (Figs. 13 and 14). These sensilla have a thick perforated cuticular wall ($310\text{--}450\text{ nm}$), although pore density seems to be less than sensilla basiconica types II and III.

Sensilla Basiconica (Type II). These sensilla have a distinct grooved surface and arise from an “eyelid”-shaped socket (Fig. 15). A single pore opening on the flagellar surface, separate from the main body of the sensilla ($\approx 0.5\text{--}1\text{ }\mu\text{m}$ in diameter), is often observed at one side of the socket base. The sensilla measure $\approx 18\text{ }\mu\text{m}$ in length and have basal diameters ranging from 2.3 to $2.4\text{ }\mu\text{m}$. These grooved sensilla terminate in a smooth but blunt ending, papillae-like tip. They are located among sensilla basiconica (type III) on the raised edge of the most distal eight flagellomeres of male and female *A. planipennis* (Figs. 3 and 16).

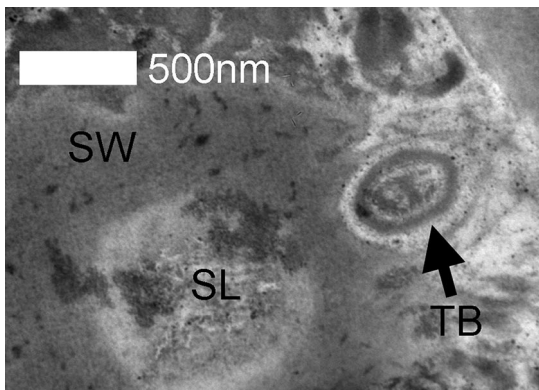


Fig. 6. Transmission electron micrograph showing a transverse section just below the base of a typical sensilla chaetica of *A. planipennis*. Note how the tubular body (TB) interacts with the base of the sensilla wall (SW). No dendrites are seen within the sensilla lumen (SL) (magnification, $25,000\times$).

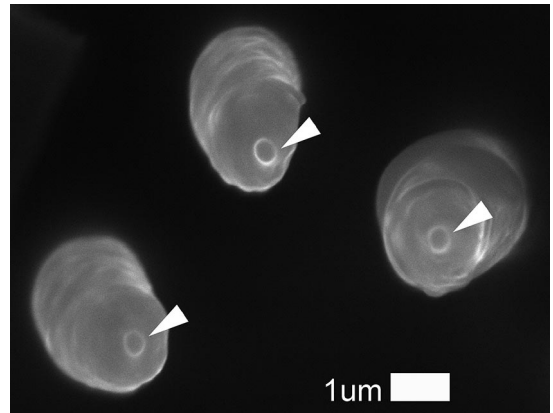


Fig. 8. Scanning electron microscope image of three uniporous sensilla on the eighth flagellomere of male *A. planipennis*. White arrowheads indicate single oval pores at the tips.

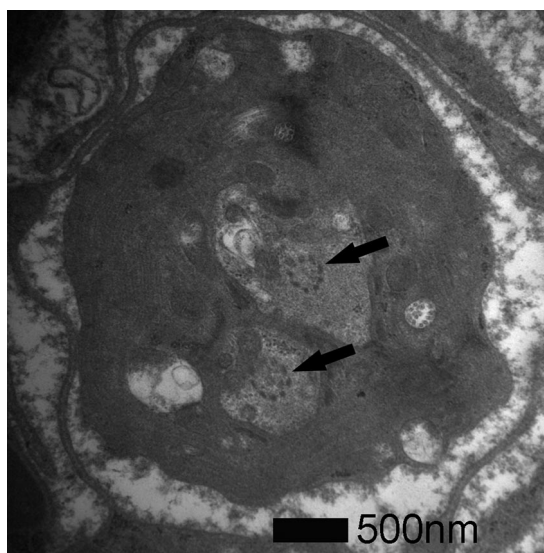


Fig. 9. Transmission electron micrograph of *A. planipennis* showing a transverse section of a uniporous sensillum cut in the vicinity of the ciliary constriction. Black arrows indicate two sensory dendrites. The ciliary regions seem to have a typical 9 by 2 by 0 arrangement (Zacharuk 1980) (magnification, 16,000 \times).

Counts on both male and female antennae (Table 1) were not significantly different ($P > 0.05$; t -test).

At the base of the sensilla, the cellular components are made up of three sensory neurons, encased in a dendritic sheath (Fig. 17). These dendrites then form

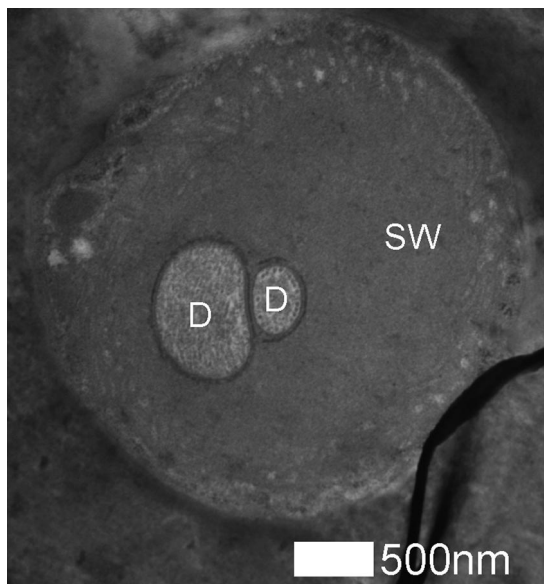


Fig. 10. Transmission electron micrograph of *A. planipennis* showing a subapical transverse section of a uniporous sensillum. The lumen is split into two canals each containing a dendrite (D). The thick sensilla wall (SW) is nonporous (magnification, 12,500 \times).

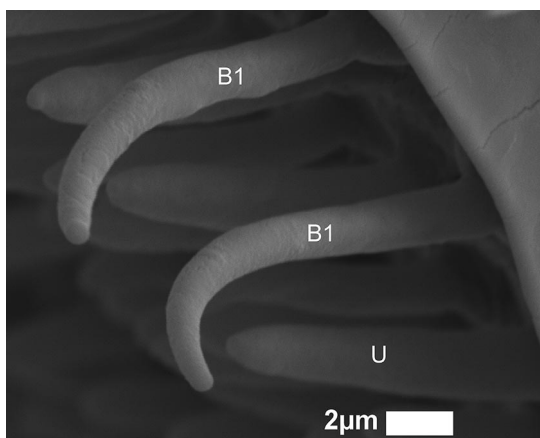


Fig. 11. Scanning electron micrograph of *A. planipennis* showing sensilla basiconica type I (B1) and a uniporous sensilla (U) along the perimeter of an apical depression (male, 10th flagellar segment).

up to 35 multiple branches (each containing varying numbers of microtubules), which run up the remaining length of the sensilla (Fig. 18). The cuticular wall is 60–80 nm in thickness and perforated by numerous pores (Fig. 18).

Sensilla Basiconica (Type III). These sensilla are similar to sensilla basiconica type II in size ($\approx 15 \mu\text{m}$ in length, 2.3–2.4 μm in diameter at the base), number, and location. When observed under the scanning electron microscope, they seem to lack the noticeable grooved surface of sensilla type II (Figs. 16 and 19). These sensilla have a fairly smooth surface and, like the type II sensilla, arise from an “eyelid”-shaped socket associated with a pore opening at the base (Fig. 19). Numbers were similar on both male and female *A. planipennis*, although significantly more sensilla ($P <$

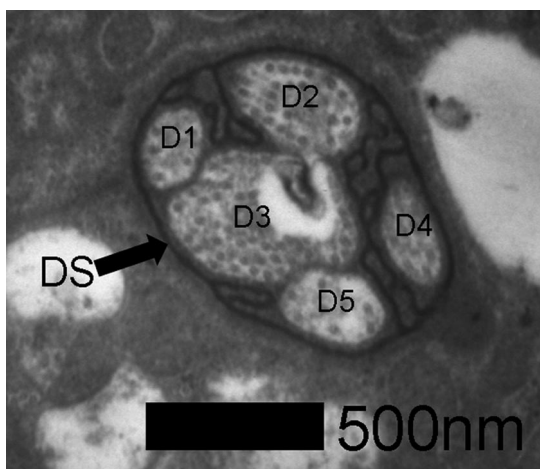


Fig. 12. Transmission electron micrograph of *A. planipennis* showing a transverse section of a sensilla basiconica (type 1). Five proximally cut dendrites (D1–D5) are surrounded by a cuticular dendritic sheath (DS) (magnification, 25,000 \times).

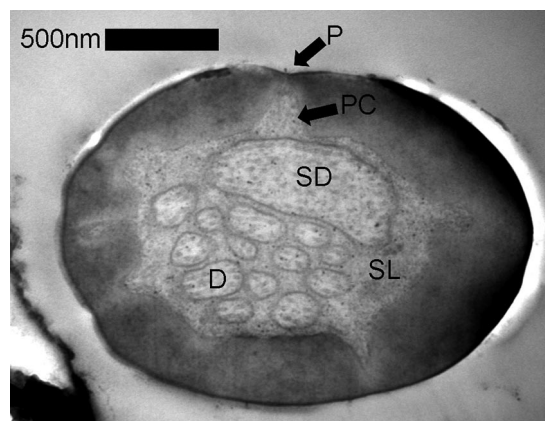


Fig. 13. Transmission electron micrograph showing a transverse, proximally cut section of a sensilla basiconica type I. Note the multiple dendritic branching (D) within the sensilla lumen (SL). One dendrite seems to have become swollen (SD) midway up the length of the sensilla. Wide pore canals (PC) are clearly seen beneath each pore opening (P), although pore tubules are not distinguishable in section (magnification, 25,000 \times).

0.05; *t*-test) were counted on the 4th and 8th most proximal flagellomeres of male antennae (Table 1).

At the base of the sensilla, the cellular components are made up of three sensory neurons, encased in a dendritic sheath (Fig. 20). Dendritic branching did occur once the dendrites entered the hair shaft of a

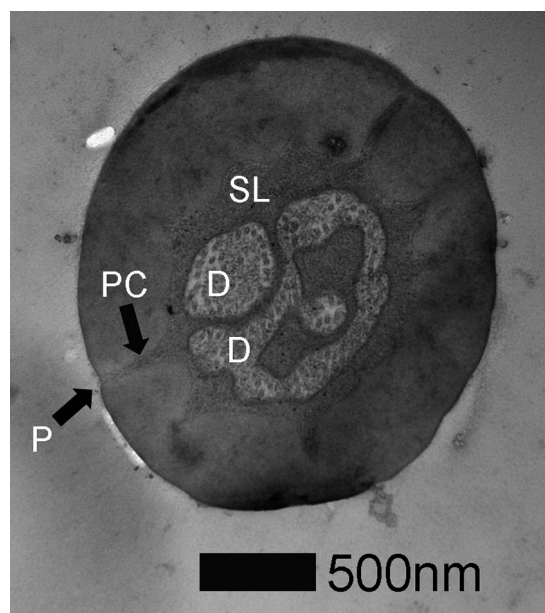


Fig. 14. Transmission electron micrograph showing a transverse, distally cut section of a sensilla basiconica type I. The branching dendrites (D) seem to fuse into one another near the sensilla tip. Pores (P) are still evident, but pore canals (PC) seem to get thinner nearer the distal tip of the sensilla (magnification, 20,000 \times).

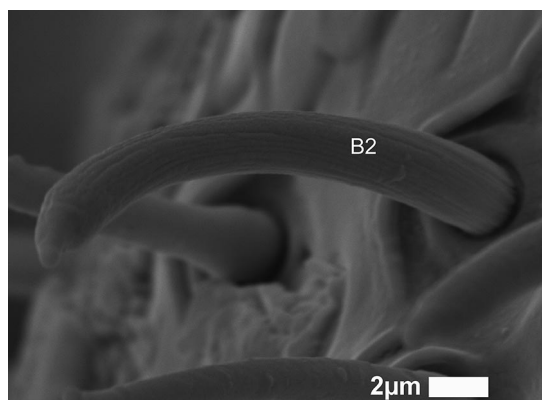


Fig. 15. Scanning electron micrograph of sensilla basiconica type II (B2) on the eighth flagellomere of a male *A. planipennis* antenna.

sensillum but to a lesser degree than the sensilla basiconica type II (between five and 13 branches). Branched dendrites contained varying numbers of microtubules. In all distally cut sections examined (sectioned ≈ 4 – $5\ \mu\text{m}$ from the tip), one dendrite was seen to swell and fill most of the lumen space (Fig. 21). The cuticular wall is 90–110 nm thick and perforated by numerous pores (Fig. 21).

Discussion

There is no obvious sexual dimorphism with respect to sensilla type or their distribution for *A. planipennis*. The only difference between the sexes is that males seem to have noticeably more uniporous gustatory/taste sensilla than females. This suggests that short range, contact cues are important for mate recognition, particularly by males. A contact chemical cue has been suggested in field assays by Lelito et al. (2007) because male *A. planipennis* spent significantly more time attempting to copulate with dead females than males or solvent-washed females. Lelito et al. (2007) also reported that *A. planipennis* seem to use contact cues for male–male repellency, because males that landed on unwashed males spent less time on them than other treatments. For other buprestids, mate location has been shown to be facilitated by host selection, followed by visual, tactile, and possibly auditory cues rather than using pheromones over any distance (Carlson and Knight 1969, Gwynne and Rentz 1983).

Flagellar pits or depressions (also referred to as fossae) containing fields of sensilla are common among buprestid species and have been used for the systematics and classification of the group (Bellamy 1985; Volkovitsh 1990, 2001). A detailed evaluation of the taxonomic value of buprestid antennal structures, examining 412 species from 316 genera of all the subfamilies of Buprestidae and six genera of other Elateriformia (using scanning electron microscopy) was done by Volkovitsh (2001). The morphology of *A. planipennis* is in agreement with the study by Volkovitsh (2001), in that buprestid species with serrate-

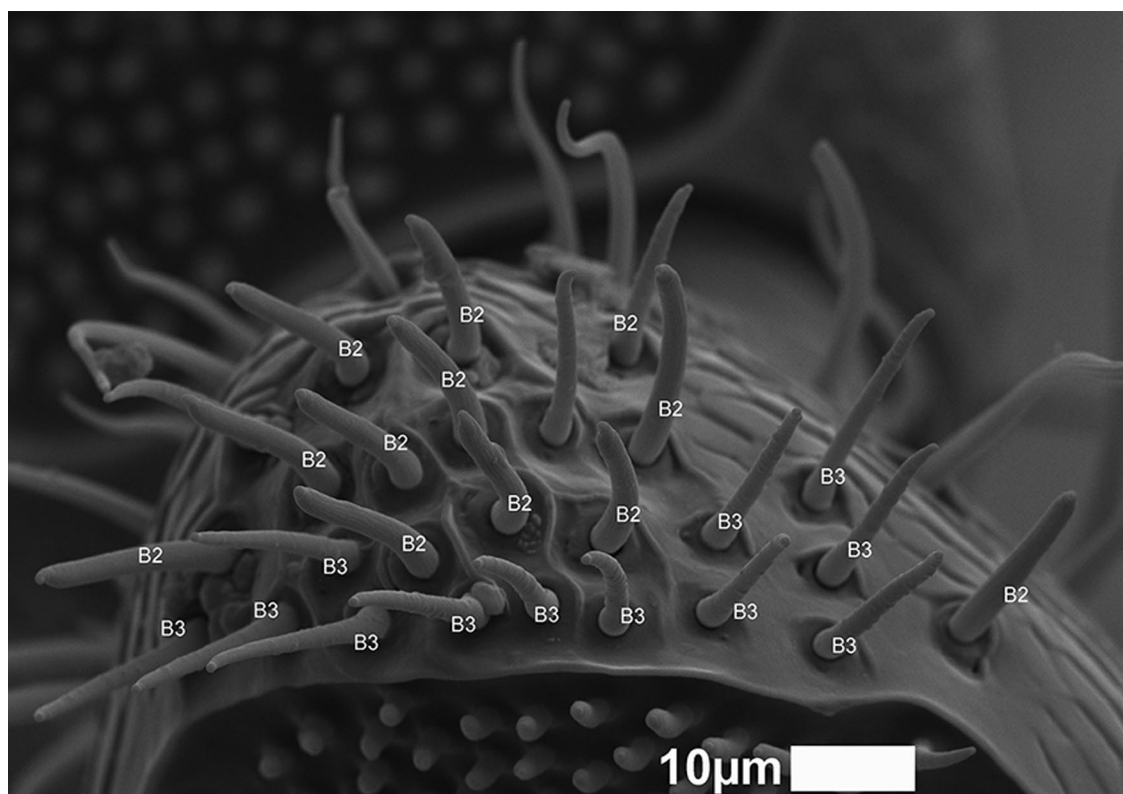


Fig. 16. Scanning electron micrograph of *A. planipennis* showing the distribution of sensilla basiconica type II (B2) and type III (B3) on the distal tip of a flagellomere (male, eighth).

truncate or elongated rectangular antennomeres bear apical pits or cavities that contain extensive sensillary fields. Throughout the numerous examples shown by

Volkovitch (2001) uniporous sensilla and several types of sensilla basiconica seem to be the dominant sensory apparatus. For a variety of insects, contact chemosensilla play an important role in accepting or rejecting food, or an oviposition substrate (Städler 1984). Be-

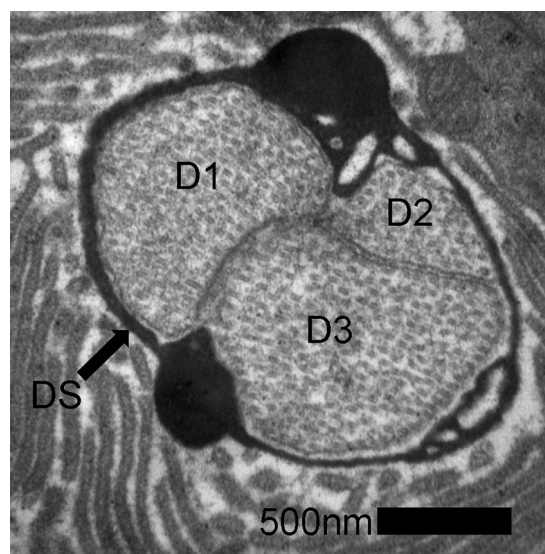


Fig. 17. Transmission electron micrograph of *A. planipennis* showing a transverse section of a sensilla basiconica (type II). Three proximally cut dendrites (D1–D3) are surrounded by a cuticular dendritic sheath (DS) (magnification, 25,000 \times).

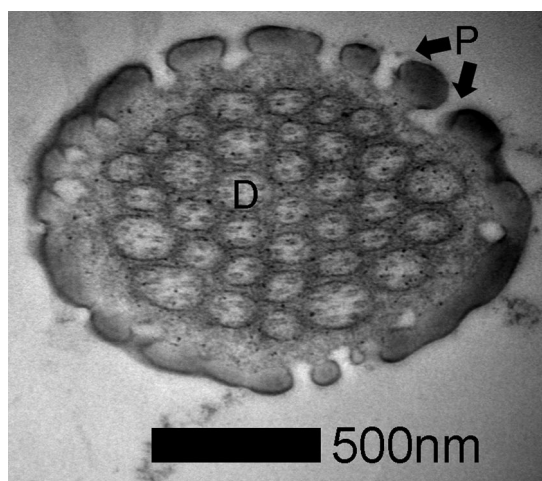


Fig. 18. Transmission electron micrograph of *A. planipennis* showing a transverse, distally cut section of a sensilla basiconica type II. The lumen is completely filled with branched dendrites (D). Numerous pores (P) can be seen in section (magnification, 31,500 \times).

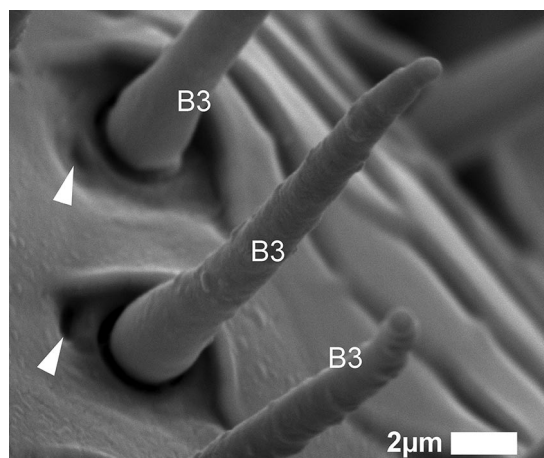


Fig. 19. Scanning electron micrograph of *A. planipennis* sensilla basiconica type III (B3) on the eighth flagellomere of a male antenna. White arrowheads indicate single pore opening at the socket base.

cause *A. planipennis* females also possess uniporous sensilla fields, their role in host location/recognition should not be discounted. The uniporous sensilla of *A. planipennis* possess the characteristics of "gustatory" or "contact chemoreceptors" as defined by Altner and Prillinger (1980), Chapman (2003), and Zacharuk (1980) in that there are a small number of sensory neurons inside a cuticular cone of cuticle, which terminate in a single pore at the tip. Stimulating chemicals reach the dendrites through this terminal pore during contact (Chapman 2003). Basal neurons that terminate in a tubular body are associated with mechanical rather than chemical stimuli (Keil and Steinbrecht 1984) and are a main characteristic of mechanoreceptors (as seen in our sections of *A. planipennis*

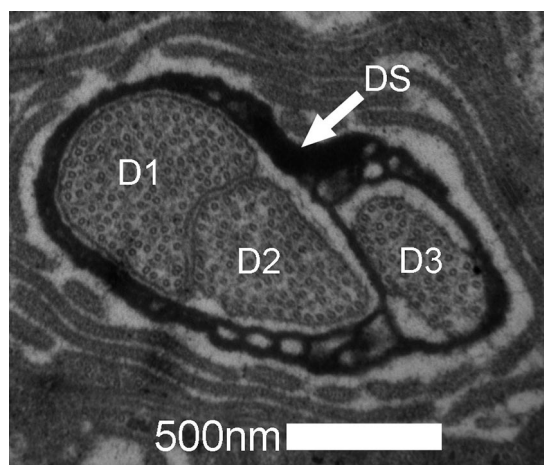


Fig. 20. Transmission electron micrograph of *A. planipennis* showing a transverse section of a sensilla basiconica (type III) cut just below the base of the sensilla. Three proximally cut dendrites (D1–D3) are surrounded by a cuticular dendritic sheath (DS) (magnification, 31500 \times).

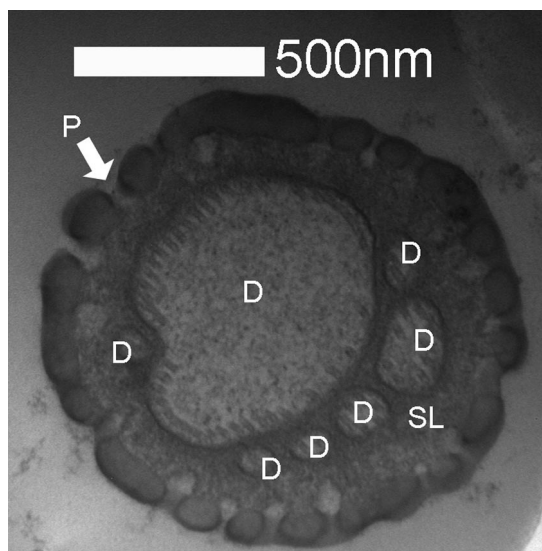


Fig. 21. Transmission electron micrograph of *A. planipennis* showing a transverse section cut $\approx 2\text{--}3\text{ }\mu\text{m}$ from the tip of a sensilla basiconica type III. Note the limited dendritic branching (D) with one dendrite becoming swollen so much that it fills most of the sensilla lumen (SL). Numerous pores (P) are present within the cuticular wall (magnification, 31,500 \times).

aporous sensilla). They can sometimes be associated with uniporous sensilla (e.g., *Culicoides impunctatus* Goetghebuer), thus allowing them to have a dual role as both mechano- and chemosensilla (Blackwell et al. 1992). In our sections of uniporous gustatory/taste sensilla, we did not observe a tubular body interacting with the base of each structure, so we prefer to define them as uniporous chemosensilla rather than uniporous contact-chemosensilla.

Recent electrophysiological studies have shown that male and female *A. planipennis* show antennal responses to a wide range of ash leaf and bark released volatiles (Rodriguez-Saona et al. 2006; Crook et al. 2006, 2008). Rodriguez-Saona et al. 2006 found that although both sexes responded to the same *F. mandshurica* volatiles, males sometimes gave stronger antennal gas chromatography-electroantennographic detection (GC-EAD) responses than females. Crook et al. (2006, 2008) showed that male and female *A. planipennis* both gave similar GC-EAD responses to the same six bark volatiles from green ash (*Fraxinus pennsylvanica* Marsh.). Lures based on these ash volatiles have enhanced trap catch of adult males and females in the field (Crook et al. 2006, 2008; Poland and McCullough 2006a,b). The physiology of the three multiporous sensilla found on *A. planipennis* have characteristics typical of sensilla that respond to olfactory stimuli (Altner and Prillinger 1980). We therefore hypothesize that the three types of multiporous sensilla (sensilla basiconica I, II, and III), are the main olfactory apparatus for detecting host tree volatiles for both male and female *A. planipennis*.

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